Indian Farmer
Volume 13, Issue 10, 2026, Pp. 581-590
Available online at: www.indianfarmer.net
ISSN: 2394-1227 (Online)

Original Article

OPEN ACCESS

Epitranscriptomics in Parasites: Molecular Regulation of Development, Survival and Pathogenesis

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Received: 04/10/2026 *Accepted on:10/10/2026*

ABSTRACT

Parasites survive in some of the most challenging biological environments known to living organisms. During their life cycles they may move between hosts, vectors, tissues and markedly different physiological conditions, yet they must continuously adjust gene expression without changing their underlying DNA sequence. A growing body of evidence indicates that RNA modifications provide an important layer of this regulation. This field, known as epitranscriptomics, examines chemical changes to RNA and their consequences for RNA stability, translation, processing, localization and fate. Among the best studied marks are N6-methyladenosine (m6A), 5-methylcytosine (m5C), N1-methyladenosine (m1A), pseudouridine (Ψ), N7-methylguanosine (m7G), N4-acetylcytidine (ac4C), uridylation and RNA editing. In parasitic protozoa, these modifications are increasingly linked with developmental transitions, differentiation, host adaptation, immune evasion and survival under stress. Studies in Plasmodium, Trypanosoma, Toxoplasma and Entamoeba illustrate how RNA chemistry can influence parasite fitness and host–parasite interactions. The emerging field also raises an important translational question: can parasite-specific RNA-modifying enzymes or modification pathways be exploited for diagnosis, drug development and control? This article introduces the principles of epitranscriptomics, highlights evidence from important parasitic organisms, and discusses future opportunities in veterinary and medical parasitology.

***Keywords*:** Epitranscriptomics; RNA modification; m6A; pseudouridine; host–parasite interaction

INTRODUCTION: LOOKING BEYOND DNA

For decades, the central dogma provided the basic framework for understanding how biological information moves from DNA to RNA and then to protein. That framework remains fundamental, but it does not fully explain how cells respond so rapidly to developmental signals, environmental stress or infection. RNA is not simply an intermediate copy of DNA. After transcription, RNA molecules can be chemically modified, structurally remodelled, transported to particular cellular locations,

translated with different efficiencies, or selectively degraded. Together, these processes create an additional regulatory layer between the genome and the proteome (Cerneckis *et al*., 2023).

Epitranscriptomics refers to the study of chemical modifications and editing events occurring on RNA and their biological consequences. Like epigenetic regulation of DNA, RNA modification can alter gene expression without changing the nucleotide sequence itself. Because many RNA modifications are dynamic and reversible, they can provide a rapid means of adjusting gene expression. This feature is particularly attractive in parasites, whose survival depends on switching between developmental stages and adapting to changing host or vector environments (Frye *et al*., 2018; Cerneckis *et al*., 2023).

Interest in parasite epitranscriptomics has expanded considerably with advances in RNA sequencing, mass spectrometry, molecular genetics and computational biology. Evidence from major human parasites suggests that RNA modifications are not merely chemical decorations; they can affect parasite development, RNA turnover, translation, differentiation and virulence. The implications for veterinary parasitology are equally important, although the field remains comparatively young (Catacalos *et al*., 2022; Guo *et al*., 2024).

What Makes an RNA Modification Biologically Important?

An RNA modification becomes biologically meaningful when it changes what happens to an RNA molecule. A modification may alter the shape of an RNA transcript, protect it from degradation, change its interaction with RNA-binding proteins, influence ribosome recognition, affect translation, or determine whether the transcript is retained, transported or destroyed. The outcome depends on the type and position of the modification and on the proteins that recognize it (Frye *et al*., 2018; Cerneckis *et al*., 2023).

A useful way to understand this system is through the concept of RNA-modifying enzymes and modification-recognition proteins. Writers are enzymes that install particular modifications. Erasers remove selected reversible modifications, whereas modification-recognition proteins recognize modified RNA and translate the chemical mark into a functional outcome. Some RNA modifications also involve additional modifying enzymes whose activities influence the final chemical state. This dynamic system gives parasites a flexible mechanism for controlling RNA fate (Frye *et al*., 2018; Cerneckis *et al*., 2023).

Major RNA Modifications

N6-Methyladenosine (m6A)

m6A is one of the most extensively studied internal modifications of RNA. It is formed by methylation at the N6 position of adenosine and is found in a broad range of organisms. In many eukaryotic RNAs, m6A is enriched around coding regions, stop codons and 3' untranslated regions. Its effects are mediated by a network of RNA-modifying enzymes and modification-recognition proteins. Writer complexes containing METTL3 and METTL14 install the mark, while enzymes such as FTO and ALKBH5 can remove it. YTH-domain proteins and other RNA-binding proteins can recognize modified transcripts and influence their stability, processing or translation (Frye *et al*., 2018; Cerneckis *et al*., 2023).

In parasites, m6A has attracted particular attention because parasite life cycles require tightly controlled changes in gene expression. The modification can therefore act as a molecular switch or rheostat, helping determine which transcripts remain stable and which are translated at different developmental stages (Catacalos *et al*., 2022; Guo *et al*., 2024).

5-Methylcytosine (m5C)

m5C is generated by methylation of cytosine and occurs in several classes of RNA, including transfer RNA, ribosomal RNA, messenger RNA and small non-coding RNA. It can influence RNA stability, structure, export and translation. Enzymes of the NSUN family and DNMT2-related pathways are among the proteins associated with RNA cytosine methylation (Catacalos *et al*., 2022; Cerneckis *et al*., 2023).

Evidence from Plasmodium indicates that m5C is relevant to parasite differentiation. In particular, NSUN2-mediated modification has been associated with transcript stability and gametocyte development, illustrating how a chemical change on RNA can influence the transmission stage of a parasite (Liu *et al*., 2022).

N7-Methylguanosine (m7G) and N1-Methyladenosine (m1A)

m7G is best known as part of the 5′ cap of eukaryotic mRNA, where it contributes to RNA stability and translation initiation. It is also present in tRNA and other RNA species, where it contributes to RNA processing and function. M7G methylation writer complexes include METTL1 for tRNA; CMTR1 and CMTR2 for mRNA cap methylation. m1A, in contrast, involves methylation at the N1 position of adenosine and has been detected in tRNA, rRNA, mRNA and long non-coding RNA. Depending on its position, m1A can influence RNA structure and translation. Writer enzymes involved in m1A are TRMT10C and TRMT61B. These modifications are of growing interest in parasites because their modifying enzymes may differ in sequence, regulation or accessibility from host counterparts (Cerneckis *et al*., 2023; Catacalos *et al*., 2022).

Pseudouridine (Ψ)

Pseudouridine is an isomer of uridine produced by conversion of a uridine residue rather than by addition of a new nucleotide. It is widely distributed among stable RNAs and has also been detected in messenger RNA. Pseudouridylation can be guided by small nucleolar RNA-containing complexes (snoRNA) or carried out by specific pseudouridine synthases (Cerneckis *et al*., 2023).

The modification can strengthen RNA structure and influence RNA-RNA and RNA-protein interactions. In parasites, this is especially relevant to ribosomal, transfer and spliceosomal RNAs that must function reliably as the organism moves between hosts with different temperatures and cellular environments (Rajan *et al*., 2019; Maran *et al*., 2021).

A-to-I RNA Editing

A-to-I editing is chemically different from methylation. It involves deamination of adenosine to inosine, mainly through adenosine deaminase acting on RNA (ADAR) enzymes. Because inosine can be interpreted similarly to guanosine by cellular machinery, editing can alter RNA sequence information, splicing, RNA structure and interactions with regulatory molecules. Although much of

the mechanistic knowledge comes from mammalian systems, RNA editing represents an important additional concept within the broader epitranscriptomic profile and deserves further investigation in parasites (Cerneckis *et al*., 2023; Yang *et al.,* 2006).

N4-Acetylcytidine and Uridylation

N4-acetylcytidine (ac4C) is an RNA acetylation mark found in rRNA, tRNA and mRNA. NAT10 is a major enzyme associated with its installation, and studies in other systems indicate that ac4C can influence RNA stability and translation. Compared with m6A, the biology of ac4C is less completely understood, particularly with respect to its modification-recognition proteins and RNA demodifying enzymes (Cerneckis *et al*., 2023).

Uridylation involves the non-templated addition of uridine residues to the 3′ end of RNA. Depending on the RNA substrate and the length of the added tail, uridylation can influence RNA maturation, stability, translation or degradation. It is therefore better viewed as a regulatory RNA-end modification than as a simple chemical label. The diversity of uridylation pathways also illustrates how parasites may use RNA metabolism to control the lifetime of transcripts (Cerneckis *et al*., 2023).

Why Epitranscriptomics Matters So Much to Parasites

Parasites are unusually dependent on precise temporal control of gene expression. A single organism may pass through morphologically and metabolically distinct stages, often in different hosts or tissues. For example, Plasmodium alternates between mosquito and vertebrate hosts, *Trypanosoma brucei* switches between insect and bloodstream forms, and *Toxoplasma gondii* alternates between replicative and chronic stages. These transitions demand large changes in RNA production, processing and translation (Catacalos *et al*., 2022; Guo *et al*., 2024).

Epitranscriptomic regulation offers a mechanism for making these changes rapidly. Instead of rewriting the genome, a parasite can modify selected RNA molecules and alter their stability or translation. This provides a potentially efficient way to respond to temperature, nutrient availability, oxidative stress, immune pressure and other environmental signals. (Catacalos *et al*., 2022; Guo *et al*., 2024).

Evidence from Important Parasitic Protozoa

Plasmodium: RNA Regulation Across the Malaria Life Cycle

Plasmodium falciparum provides one of the clearest examples of stage-associated RNA modification. Transcriptome-wide studies have shown extensive m6A methylation during blood-stage development. The abundance and distribution of m6A-associated transcripts change during parasite development, supporting the idea that RNA modification participates in stage-specific regulation (Baumgarten *et al*., 2019).

m6A modification-recognition proteins are also functionally important. PfYTH-family proteins show stage-associated expression, and functional studies of PfYTH.2 have linked the reader to translational control. These findings suggest that the m6A system is not simply marking transcripts;

it is part of a regulatory pathway connecting RNA chemistry with parasite development (Sinha *et al*., 2021).

m5C provides another example. Plasmodium NSUN2-mediated modification has been associated with mRNA stability and gametocyte development. Disruption of this pathway affects the parasite's capacity to produce mature sexual stages, highlighting the potential of RNA-modifying enzymes as targets for transmission-blocking strategies. (Liu *et al*., 2022).

***Trypanosoma brucei*: Adapting to Two Very Different Hosts**

Trypanosoma brucei, the causative agent of African sleeping sickness, must adapt between the insect vector and the mammalian bloodstream. Comparative m6A methylome studies have identified differences between major life stages, indicating that RNA methylation changes as the parasite changes its biological environment (Liu *et al*., 2019; Maran *et al*., 2021).

The parasite also provides striking examples of pseudouridine biology. Pseudouridylation of spliceosomal small nuclear RNAs can influence RNA-RNA and RNA-protein interactions, while modifications in ribosomal RNA contribute to ribosome function. These pathways may help the parasite maintain efficient RNA processing and protein synthesis under the different temperatures and cellular conditions encountered in its hosts (Rajan *et al*., 2019; Maran *et al*., 2021).

Another intriguing modification is queuosine (Q) in tRNA. *T. brucei* has specialized pathways for acquiring and modifying tRNA, and Q modification has been linked to mitochondrial protein synthesis and ribosomal stability. These observations raise the possibility that nutrient availability and host-derived metabolites can become connected to parasite RNA regulation. (Maran *et al*., 2021; Catacalos *et al*., 2022).

***Toxoplasma gondii*: RNA Modification and Parasite Fitness**

Toxoplasma gondii depends on tightly regulated gene expression for intracellular replication and developmental transitions. Its m6A machinery includes METTL3, METTL14 and associated factors, and experimental depletion of components of this pathway has been linked with severe defects in parasite replication (Holmes *et al*., 2021).

m6A modification-recognition proteins also appear to contribute to RNA processing. YTH-domain proteins have been associated with 3′-end processing of pre-mRNAs, and disruption of this system compromises parasite viability. Together, these findings show that RNA modification can influence fundamental processes required for parasite survival rather than acting only during specialized developmental stages (Holmes *et al*., 2021).

Pseudouridine biology provides another layer. Studies of the pseudouridine synthase TgPUS1 have connected RNA modification with differentiation between tachyzoite and bradyzoite forms. Such observations are important because chronic infection depends on successful developmental transitions and persistence within host tissues (Anderson *et al*., 2009; Guo *et al*., 2024).

***Entamoeba histolytica*: RNA Chemistry Meets the Gut Microbiome**

Entamoeba histolytica offers an especially interesting example of how the parasite's RNA modification system can interact with its surrounding microbial environment. The parasite can

salvage queuine, a metabolite supplied by intestinal bacteria, and incorporate it into tRNA through its tRNA-guanine transglycosylase pathway (Nagaraja *et al*., 2021; Sarid *et al*., 2022).

Queuosine-modified tRNA has been associated with changes in tRNA methylation and improved responses to oxidative stress. The pathway also influences expression of genes involved in stress responses and virulence. This example broadens the concept of epitranscriptomics: parasite RNA chemistry may be influenced not only by parasite-encoded enzymes but also by metabolites obtained from the host-associated microbiota (Nagaraja *et al*., 2021; Sarid *et al*., 2022).

Epitranscriptomics and Parasite Pathogenesis

Pathogenesis is not determined solely by the presence of a parasite. Disease severity depends on parasite replication, tissue tropism, immune interactions, metabolic adaptation and the ability to persist. RNA modifications can potentially influence each of these processes by controlling transcripts that encode proteins involved in growth, invasion, stress tolerance and host interaction.

In Toxoplasma, perturbation of pseudouridine synthesis has been linked with altered developmental behaviour and disease outcomes in experimental models. In Plasmodium, tRNA cytosine methylation influences stress tolerance and can affect the production of sexual stages. In Entamoeba, queuine-dependent RNA modification pathways can alter oxidative-stress responses and virulence-associated gene expression. These examples suggest that parasite pathogenesis should increasingly be examined not only at the genomic and transcriptomic levels but also at the level of RNA chemistry (Anderson *et al*., 2009; Hammam *et al*., 2021; Nagaraja *et al*., 2021).

Host-Parasite Epitranscriptomic Interactions

Parasite infection can also modify the host epitranscriptome. This is an emerging area with potentially major implications for immunology. For example, malaria infection has been associated with changes in m6A modification patterns in host tissues, accompanied by altered expression of pathways involved in immune responses (Wang *et al*., 2022).

The relationship may therefore be bidirectional: parasites regulate their own RNA modifications while infection can reshape RNA modification pathways in host cells. Understanding this interaction could reveal mechanisms of immune manipulation and may identify host pathways that can be modulated therapeutically (Wang *et al*., 2022; Guo *et al*., 2024).

Epitranscriptomics and Drug Resistance

Drug resistance is one of the most serious challenges in parasitic disease control. Resistance is usually discussed in terms of genetic mutations, gene amplification or altered drug transport, but post-transcriptional regulation may also influence how parasites respond to treatment. Changes in RNA modification can alter the abundance or translation of proteins involved in metabolism, stress responses and drug sensitivity. Evidence linking m6A-associated pathways with parasite development and stress adaptation suggests that epitranscriptomic regulation deserves greater attention in resistance research. (Hammam *et al*., 2021; Guo *et al*., 2024).

Importantly, this does not mean that every change in RNA modification causes resistance. Establishing causality will require controlled genetic manipulation, direct mapping of RNA modifications, measurement of transcript and protein abundance, and drug-response experiments.

Could RNA Modifiers Become New Antiparasitic Targets?

The therapeutic appeal of parasite RNA-modifying enzymes lies in the possibility of selectively disrupting a process that is essential for parasite survival. If a parasite enzyme has sufficiently different structural or regulatory features from its host counterpart, it may provide a tractable drug target. (Cerneckis *et al*., 2023; Guo *et al*., 2024). Potential targets include m6A RNA-modifying enzymes and modification-recognition proteins, pseudouridine synthases, m1A-associated enzymes and other parasite-specific components of RNA modification pathways. Structural biology, molecular docking, chemical screening and parasite genetics can be combined to identify vulnerable enzyme pockets and determine whether selective inhibition is feasible (Catacalos *et al*., 2022; Guo *et al*., 2024).

However, considerable caution is required. Many RNA-modifying enzymes are conserved across eukaryotes, and indiscriminate inhibition could harm host cells. The most promising targets will therefore be those with parasite-specific catalytic features, essential functions, restricted host expression or exploitable structural differences.

Diagnostic Potential: Can RNA Modifications Become Biomarkers?

One of the most exciting possibilities is the use of epitranscriptomic signatures as biomarkers. Parasites at different developmental stages may have distinct RNA modification patterns, and drug-resistant populations may show characteristic changes. In principle, such signatures could help distinguish parasite stages, monitor treatment response or identify emerging resistance (Catacalos *et al*., 2022; Guo *et al*., 2024).

At present, this concept remains more promising than routine. Sensitive and reproducible methods are required to detect low-abundance modifications in clinical samples, distinguish parasite RNA from host RNA, and determine whether a modification is sufficiently specific for diagnostic use.

Opportunities for Veterinary Parasitology

Veterinary parasitology is an especially promising area for future epitranscriptomic research. Major veterinary parasites undergo complex developmental cycles and encounter abrupt changes in temperature, nutrition, immune pressure and tissue environment. These conditions create a strong biological rationale for RNA-based regulation (Guo *et al*., 2024; Catacalos *et al*., 2022).

Future studies could investigate RNA modifications in economically important parasites of cattle, buffaloes, sheep, goats, poultry and companion animals. Particular attention could be given to parasites in which stage conversion, persistence or drug resistance limits disease control. For example, comparative epitranscriptomic profiling of drug-sensitive and drug-resistant parasite isolates could identify candidate resistance-associated RNA marks. Similarly, mapping RNA modifications across parasite life stages could identify stage-specific regulatory enzymes that are absent or substantially different in the host.

What Comes Next?

The next phase of parasite epitranscriptomics should move from descriptive mapping toward functional biology. It is no longer enough to identify that an RNA modification is present. Researchers need to determine which transcript carries the modification, which enzyme installs or removes it, which reader recognizes it, and how changing the modification alters parasite phenotype (Catacalos *et al*., 2022; Guo *et al*., 2024). Several approaches will be particularly valuable. High-resolution RNA-modification mapping can define the location of individual marks. Single-cell approaches can reveal heterogeneity within parasite populations. Long-read sequencing may help connect modifications with complete transcript structures and isoforms. Proteomics can establish whether RNA changes are translated into altered protein abundance, while metabolomics can identify environmental signals that influence RNA modification (Cerneckis *et al*., 2023; Guo *et al*., 2024).

Integration with genomics, transcriptomics, proteomics and metabolomics will ultimately provide a more complete picture of parasite biology. Such multi-omics approaches may reveal regulatory networks that cannot be recognized from any single data type (Catacalos *et al*., 2022; Guo *et al*., 2024).

Challenges and Research Gaps

Despite rapid progress, several limitations remain. First, the presence of a modification does not automatically demonstrate its biological function. Second, many current techniques have limitations in site resolution, sensitivity or quantitative accuracy. Third, parasite RNA is often present in small quantities relative to host RNA in clinical samples, making parasite-specific measurements technically demanding (Cerneckis *et al*., 2023; Catacalos *et al*., 2022).

Another challenge is the uneven distribution of knowledge among parasite species. A small number of model parasites have been studied extensively, whereas many veterinary parasites remain almost unexplored. This creates an opportunity for veterinary research groups to establish foundational epitranscriptomic maps in neglected parasite species (Guo *et al*., 2024).

CONCLUSION

Epitranscriptomics adds a new dimension to the study of parasite biology. DNA provides the information required to build a parasite, but RNA modifications help determine when, where and how that information is used. Evidence from Plasmodium, Trypanosoma, Toxoplasma and Entamoeba demonstrates that RNA chemistry can influence development, differentiation, stress tolerance, host adaptation and virulence (Baumgarten *et al*., 2019; Liu *et al*., 2019; Holmes *et al*., 2021; Nagaraja *et al*., 2021; Guo *et al*., 2024). For parasitology, the field is still young, but its potential is considerable. RNA-modifying enzymes may eventually provide new therapeutic targets, while stage-specific or resistance-associated RNA signatures could support improved diagnostics and surveillance. The greatest opportunity lies in moving from cataloguing modifications to understanding their function and exploiting parasite-specific vulnerabilities (Catacalos *et al*., 2022; Guo *et al*., 2024).

In veterinary parasitology, this transition could be particularly valuable. Many important animal parasites remain poorly characterized at the post-transcriptional level. Systematic

epitranscriptomic studies could therefore uncover previously unrecognized mechanisms of persistence, drug resistance and pathogenicity, ultimately contributing to better prevention, diagnosis and control of parasitic diseases. (Guo *et al*., 2024).

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